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Secondary production estimates were calculated for selected net-spinning caddisflies from an Ozark stream using the size-frequency method. Combined production for all species studied was estimated to be 2.64 g/m²/yr (dry mass). *Chimarra obscura* and *Cheumatopsyche* spp. were the most abundant caddisfly species (N = 18/m² and 19/m², respectively) contributing 48% and 47%, respectively, to total production. *Chimarra aterrima*, *Polycentropus centralis* and *Mormaldia moesta* contributed the remaining 5%. Annual P/B ratios ranged from 5 for the univoltine *M. moesta* to the 11.5 for the bivoltine *P. centralis*. A P/B ratio of 17 was estimated for *Cheumatopsyche* spp., but this large value was attributed to grouping at least four ecologically similar but distinct species. Annual mean production for some species was similar to estimates reported in other studies, but production for all species was considerably lower than estimates from other lotic ecosystems.

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SECONDARY PRODUCTION OF NET-SPINNING CADDISFLIES
(TRICHOPTERA: CURVIPALPIA) IN AN OZARK STREAM^a

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ABSTRACT

Secondary production estimates were calculated for selected net-spinning caddisflies from an Ozark stream using the size-frequency method. Combined production for all species studied was estimated to be $2.64 \text{ g/m}^2/\text{yr}$ (dry mass). Chimarra obscura and Cheumatopsyche spp. were the most abundant caddisfly species ($N = 18/\text{m}^2$ and $19/\text{m}^2$, respectively) contributing 48% and 47%, respectively, to total production. Chimarra aterrima, Polycentropus centralis and Wormaldia moesta contributed the remaining 5%. Annual P/\bar{B} ratios ranged from 5 for the univoltine W. moesta to the 11.5 for the bivoltine P. centralis. A P/\bar{B} ratio of 17 was estimated for Cheumatopsyche spp., but this large value was attributed to grouping at least four ecologically similar but distinct species. Annual mean production for some species was similar to estimates reported in other studies, but production for all species was considerably lower than estimates from other lotic ecosystems.

INTRODUCTION

The filter-feeding or net-spinning caddisflies are restricted to the infraorder Curvivalpia which includes the families Hydropsychidae, Philopotamidae, Polycentropodidae, and Psychomyiidae (Weaver and Morse 1986, Wiggins

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1977). Most curvivalprians construct fixed retreats of various materials and designs equipped with seine-like catchnets composed of silken threads (Wallace and Malas 1976, Wiggins 1977) used to filter food particles from the water column. The abundance and diversification of immature net-spinning caddisflies in most freshwater streams are evidence that they play a major role in energy transfer in those ecosystems.

Secondary production, or the elaboration of animal tissue per unit time, is a measure of the relative importance of a species (population) to the aquatic ecosystem as a whole because production is the means by which energy is made available for transfer from one trophic level to another. Estimating production of an animal population is essential to understanding the role of a population in energy flow pathways (Benke and Wallace 1980).

Although aquatic insect production studies have been reported from throughout the world, most have been conducted in North America. Lentic systems, Appalachian headwater streams, and blackwater streams of the southeastern United States have been the most commonly studied habitats. By contrast, only a few production studies have been conducted in the Ozarks region of Arkansas, Missouri and Oklahoma where Bowles (1990), Gordon (1987), Jop and Stewart (1987), and Sullivan and Topping (1984) reported production estimates for Megaloptera, Gastropoda, Plecoptera, and Ephemeroptera, respectively. Comparative information on production estimates for a given species from different geographical regions and habitats is limited.

This investigation was conducted to estimate secondary production for a group of curvivalprian caddisflies from the Mulberry River in northwestern Arkansas.

METHODS AND MATERIALS

A third-order reach of the Mulberry River, Johnson County, Arkansas was selected for study. Riparian canopy was well developed, and the terrestrial

plant community was quite diverse. Substrate at the study site was chiefly pebble and cobble with a few large boulders were scattered within the stream channel. Water temperature ranged from 6 to 32 °C, and current velocity and point discharge ranged from 0.26 to 2.34 m/sec and 0.10 to 13.75 m³/sec, respectively. The river maintained continuous base flow throughout the study duration. A more detailed description of the study area can be found in Bowles (1989, 1990).

Benthic samples were collected randomly from riffles with a modified Hess sampler (0.1 m², 243 µm mesh) from August 1985 to August 1986. On each sampling date, 24 samples were collected. Samples were collected twice monthly from May through October and monthly from November through March. No collections were made during April due to high water levels. Samples were preserved in the field with 10% formalin and transported to the laboratory where they were sorted using 10X magnification. All trichopteran larvae and pupae were removed, identified to the lowest possible taxonomic level, sorted by larval instar and counted. Species collected and identified in this study included Chimarra aterrima (Hagen), C. obscura (Walker), Polycentropus centralis Banks, Wormaldia moesta (Banks), and Cheumatopsyche spp. Larvae of Cheumatopsyche were not identified to species and therefore data were grouped for the genus.

A selected number of each larval instar was dried at 100 °C for 24 h, cooled in a desiccator for an additional 24 h, and weighed. Specimens were selected from samples throughout the sampling period to estimate the mean annual weight for each instar of a given species (Mackay 1984). Mean individual weights were calculated as geometric means (Sokal and Rohlf 1981).

Secondary production was calculated using the size-frequency method (Benke 1984), and production estimates were corrected by the cohort production interval (CPI) (Benke 1979, 1984). Portions of the life cycle not spent in

productive stages, including eggs until hatching and pupal periods were subtracted from the life history length to arrive at the CPI. Life histories of the species examined in this study were reported by Bowles (1989). Data on egg and pupal developmental periods were obtained from the literature (Anderson and Wallace 1984, Cudney and Wallace 1980, MacFarlane and Waters 1982, Singh et al. 1984, Wiggins 1977).

RESULTS AND DISCUSSION

Mean individual weight and associated statistics for each larval instar of each species are shown in Table 1. Table 2 shows comparisons of annual mean density, mean standing stock biomass, production, and annual P/\bar{B} ratios for each species. All of the species studied, exclusive of W. moesta, were bivoltine and estimated to have a CPI of 5 months; the univoltine W. moesta had a CPI of 11 months (Bowles 1989).

Early instar larvae, particularly the first, of all species studied were occasionally under-represented in samples. In secondary production calculations, under-represented larval instars result in negative weight lost values for that size class (Benke 1984, Waters and Crawford 1973), and because negative production is not theoretically possible, negative weight lost values were not included in the production estimates reported here. The effect of excluding negative weight lost values from the production total of each species is negligible because early instars compose only a very small amount of the total production for a given species (Kimerle and Anderson 1971). In this study, 97% of the total production of C. obscura was contributed by instars III-V. Thus, under-representation of first-instars was of little consequence in the overall production of the species.

Under-representation of early instars in production studies has been a common problem (Benke and Wallace 1980, Cudney and Wallace 1980, Freeman and Wallace 1984, Mackay and Waters 1986, Short et al. 1987, Waters and Crawford

Table 1. Mean individual weight and associated statistics of larval instars of selected curvialpian caddisfly species collected from the Mulberry River, Arkansas.

Species	Instar	N	Mean Individual ^a Weight (g)	S _{\bar{x}}
<u>Cheumatopsyche</u> spp.	I	140	0.00002	0.00002
	II	120	0.00005	0.00005
	III	60	0.00018	0.00022
	IV	48	0.00061	0.00007
	V	26	0.00130	0.00147
<u>Chimarra aterrima</u>	I	59	0.00004	0.00005
	II	78	0.00011	0.00012
	III	53	0.00026	0.00026
	IV	36	0.00065	0.00160
	V	41	0.00134	0.00238
<u>C. obscura</u>	I	340	0.00002	0.00002
	II	323	0.00012	0.00015
	III	277	0.00033	0.00010
	IV	176	0.00070	0.00047
	V	172	0.00110	0.00011
<u>Polycentropus centralis</u>	I	28	0.00007	0.00013
	II	40	0.00010	0.00012
	III	32	0.00017	0.00020
	IV	12	0.00069	0.00080
	V	8	0.00094	0.00108
<u>Wormaldia moesta</u>	I	49	0.00002	0.00002
	II	8	0.00028	0.00040
	III	10	0.00033	0.00047
	IV	6	0.00064	0.00090
	V	6	0.00155	0.00219

^a Oven dry mass.

1973). The reasons for such under-representation are unclear but may relate to sampling inadequacy, less time spent in earlier instars (Benke and Wallace 1980), or clumped distributions of first-instar larvae attributable to female ovipositional behavior.

Total annual production for all species studied was 2.64 g/m²/yr. Among

Table 2. Secondary production estimates for net-spinning Trichoptera from the Mulberry River, Arkansas^a.

Species	N ^b (no/m ²)	B ^c (g/m ²)	p ^d (g/m ² /yr)	Annual P/ \bar{B}	CPI ^e
<u>Cheumatopsyche</u> spp.	19.04	0.070	1.24	17.02	5
<u>Chimarra aterrima</u>	0.97	0.009	0.09	10.00	5
<u>C. obscura</u>	17.68	0.110	1.26	10.36	5
<u>Polycentropus centralis</u>	0.99	0.004	0.04	11.50	5
<u>Wormaldia moesta</u>	0.29	0.002	0.01	5.00	11
			Total = 2.64 (g/m ² /yr)		

^a Size-frequency method.

^b Annual mean density.

^c Standing stock biomass; oven dry mass.

^d Annual production.

^e Cohort production interval.

species, production statistics yielded highly variable results. Production of C. obscura and Cheumatopsyche spp. was far greater than that of the other species and accounted for 47.73% and 46.97%, respectively, of the total production. The combined production of C. aterrima, P. centralis, and W. moesta accounted for the remaining 5.30% of the total production. Wormaldia moesta contributed the least biomass of all species having a production estimate of only 0.01 g/m²/yr.

Statistical confidence limits for production estimates have been developed for the size-frequency method (Krueger and Martin 1980), but the technique has been criticized because such confidence limits violate the basic assumptions

of parametric statistics (Behmer and Hawkins 1986, Morin et al. 1987), and the method for calculating variance is sensitive to changes in size distributions and fails to address the effects of the CPI (Short et al. 1987). Because of these difficulties, confidence limits are of limited use and were not used here.

Annual P/\bar{B} ratios were relatively consistent among species, and the cohort P/\bar{B} ratios (annual P/\bar{B} divided by the CPI correction factor) generally approximated the range of 2-5 suggested by Waters (1987) to be characteristic of holometabolous aquatic insects. The single exception was for Cheumatopsyche spp. which had a cohort P/\bar{B} ratio of 6.9. The larger cohort P/\bar{B} ratio estimated for Cheumatopsyche spp. probably is an artifact of the grouping of at least four distinct species: Cheumatopsyche aphantha Ross, C. campyla Ross, C. minuscula (Banks), and C. pettiti (Banks), (Bowles 1989). The immatures of these species could not be distinguished. Although these species may be ecologically similar, the potential error associated with combining several species is evident and serves to emphasize the importance of working at the specific level in secondary production studies and ecological studies in general.

Combined annual production estimates for caddisflies have been reported for other lotic systems as well. A broad range of production (12.6 to 41.4 g/m²/yr; ash-free dry weight) was reported by Cudney and Wallace (1980) for a complex of net-spinning species in the Savannah River, Georgia. Given that ash-free dry weight is approximately 90% of dry weight (Benke and Wallace 1980, Bowles, personal observation), the estimates reported by Cudney and Wallace (1980) are considerably greater than those reported for this study. However, Cudney and Wallace (1980) estimated production from snag-wood habitat rather than from stream bottom substrate and the relationship between these two different habitats is presently unclear. Similarly, Benke et al. (1984)

reported 11.89 g/m²/yr (dry weight) total production for all trichopterans collected from snag-wood habitat in the Satilla River, Georgia. Parker and Voshell (1983) reported a broad range of production, 9.4 to 325.0 g/m²/yr (dry mass; authors' conversion), for populations of net-spinning caddisflies from an impounded and free-flowing river. Also, virtually all of the cohort P/\bar{B} ratios reported by Parker and Voshell (1983) ranged between 4 and 5. Other studies, including those of Benke and Wallace (1980) and Freeman and Wallace (1984), have reported combined production estimates for net-spinning caddisflies comparable to those mentioned above.

Secondary production previously has been estimated for some species studied here (Table 3). However, comparisons among production estimates from different geographical regions are difficult because of the broad array of habitats sampled and the differing means by which larval weights have been reported. Biomass in production studies is most commonly reported as dry weight, or ash-free dry weight, but wet weight is used occasionally (Waters 1977). Voltinism also tends to confound attempts at comparing production estimates. For example, a bivoltine population of a species theoretically should produce twice the biomass/unit time of a univoltine population if both have the same mean individual weights for larval instars (Benke 1984). Production estimates, therefore, must be adjusted by the appropriate correction factor before comparisons can be made.

This study serves to provide information on secondary production of curvialpian caddisflies from a geographic area that had previously received little attention in regard to production studies. The findings of this study suggest that undisturbed Ozark streams may not be as productive for trichopterans, as similar streams in other geographic areas such as the southeastern United States. Considerable information on secondary production

Table 3. Secondary production estimates and associated information for selected curvialpian caddisflies in North America^a.

Species	Voltinism ^b	Annual ^c Production (g/m ² /yr)	Annual P/B	Location ^d	Reference ^e
<u>Cheumatopsyche</u> sp.	B	0.13**	14.7	GA	1
<u>Cheumatopsyche</u> sp.	B	0.66**	9.8	GA	2
<u>Cheumatopsyche</u> spp.	U	2.34-56.83	4.1-4.8	VA	3
<u>Cheumatopsyche</u> spp.	U	0.01-0.07	6.9	MA	4
<u>C. pettiti</u>	U	1.20-11.60	3.2-4.0	MN	5
<u>C. pettiti</u>	U	5.50-68.50*	4.4-7.0	MN	5
<u>Chimarra obscura</u>	U	0.62-2.64	3.9-5.7	VA	3
<u>Polycentropus</u> sp.	U	0.90*	3.9	MN	6
<u>Neureclipsis-</u>					
<u>Polycentropus</u> spp.	U	0.01-0.02	5.6	MA	4

^a All production estimates were calculated using the size-frequency method.

^b B = bivoltine, U = univoltine.

^c Oven dry mass unless otherwise indicated (* = wet weight, ** = ash-free dry weight).

^d State abbreviations are those used by the United States Postal Service.

^e 1. Freeman and Wallace (1984), 2. Benke et al. (1984), 3. Parker and Voshell (1983), 4. Neves (1979), 5. Mackay and Waters (1986), 6. Krueger and Waters (1983).

for Ozark streams, as well as those of other areas, needs to be gathered to provide a solid foundation by which these differing lotic ecosystems can be analyzed and compared.

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LITERATURE CITED

- Anderson, N. H., and J. B. Wallace. 1984. Habitat, life history, and behavioral adaptations of aquatic insects, pp. 38-58 In An introduction to the aquatic insects of North America, 2nd ed. R. W. Merritt and K. W. Cummins (eds.). Kendall/Hunt, Dubuque, Iowa.
- Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. *Freshwat. Biol.* 16:287-300.
- Benke, A. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanogr.* 24:168-171.
- Benke, A. C. 1984. Secondary production of aquatic insects, pp. 289-322 In *The ecology of aquatic insects*. V. H. Resh and D. M. Rosenberg (eds.). Praeger Press, New York.
- Benke, A. C., T. C. Van Arsdall, Jr., and D. M. Gillespie. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecol. Monogr.* 54:25-63.
- Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net spinning caddisflies in a southern Appalachian stream. *Ecology* 61:108-118.
- Bowles, D. E. 1989. Ecology of net-spinning caddisflies (Insecta: Trichoptera) in the Mulberry River, Arkansas, U.S.A. Unpublished Ph. D.

- Dissertation, University of Arkansas, Fayetteville, Arkansas.
- Bowles, D. E. 1990. Life history and variability of secondary production estimates for Corydalis cornutus (Megaloptera: Corydalidae) in an Ozark stream. J. Agri. Entomol. 7:61-70.
- Cudney, M. D., and J. B. Wallace. 1980. Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (U. S. A.) river. Holartic Ecol. 3:159-182.
- Freeman, M. C., and J. B. Wallace. 1984. Production of net-spinning caddisflies (Hydropsychidae) and black flies (Simuliidae) on rock outcrop substrate in a small southeastern Piedmont stream. Hydrobiologia 112:3-15.
- Gordon, M. E. 1987. Habitat utilization, population dynamics, and production of three gastropods (Prosobranchia: Pleuroceridae) from the North Fork of the White River, Missouri. Unpublished Ph. D. Dissertation, University of Arkansas, Fayetteville, Arkansas.
- Jop, K. M., and K. W. Stewart. 1987. Annual stonefly (Plecoptera) production in a second order Oklahoma Ozark stream. J. N. Am. Benthol. Soc. 6:26-34.
- Kimerle, R. A., and N. H. Anderson. 1971. Production and bioenergetic role of the midge Glyptotendipes barapiques (Staeger) in a waste stabilization lagoon. Limnol. Oceanogr. 16:646-659.
- Krueger, C. C., and F. B. Martin. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnol. Oceanogr. 25:773-777.
- Krueger, C. C., and T. F. Waters. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64:840-850.
- MacFarlane, M. B., and T. F. Waters. 1982. Annual production by caddisflies and mayflies in a western Minnesota plains stream. Can. J. Fish. Aquat. Sci. 39:1628-1635.

- Mackay, R. J. 1984. Some causes of variation in estimates of mean weights for Hydropsyche larvae (Trichoptera: Hydropsychidae). Can. J. Fish. Aquat. Sci. 41:1634-1642.
- Mackay, R. J., and T. F. Waters. 1986. Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67:1680-1686.
- Morin, A., T. A. Mousseau, and D. A. Roff. 1987. Accuracy and precision of secondary production estimates. Limnol. Oceanogr. 32:1342-1352.
- Neves, R. J. 1979. Secondary production of epilithic fauna in a woodland stream. Am. Midl. Nat. 102:209-224.
- Parker, C. R., and J. R. Voshell, Jr. 1983. Production of filter-feeding Trichoptera in an impounded and a free-flowing river. Can. J. Zool. 61:70-87.
- Singh, M. P., S. M. Smith, and A. D. Harrison. 1984. Life cycles, microdistribution, and food of two species of caddisflies (Trichoptera) in a wooded stream in southern Ontario. Can. J. Zool. 62:2582-2588.
- Short, R. A., E. H. Stanley, J. W. Harrison, and C. R. Epperson. 1987. Production of Corydalis cornutus (Megaloptera) in four streams differing in size, flow, and temperature. J. N. Am. Benthol. Soc. 6:105-114.
- Sokal, R. E., and F. J. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman and Co., San Francisco.
- Sullivan, M. D., and M. S. Topping. 1984. Secondary production in Isonychia bicolor (Ephemeroptera: Oligoneuriidae). Trans. Missouri Acad. Sci. 18:17-24.
- Wallace, J. B., and D. Malas. 1976. The fine structure of capture nets of larval Philopotamidae (Trichoptera), with special emphasis on Dolophiloides

distinctus. Can. J. Zool. 54:1788-1802.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10:91-164.

Waters, T. F. 1987. The effect of growth and survival patterns upon the cohort P/\bar{B} ratio. J. N. Am. Benthol. Soc. 6:223-229.

Waters, T. F., and G. W. Crawford. 1973. Annual production of a stream mayfly population: A comparison of methods. Limnol. Oceanogr. 18:286-296.

Weaver, J. S. III, and J. C. Morse. 1986. Evolution of feeding and case-making behavior in Trichoptera. J. N. Am. Benthol. Soc. 5:150-158.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. Toronto Press: Toronto.